THE CRANIAL MORPHOLOGY OF THE LOWER TRIASSIC DICYNODONT *MYOSAURUS GRACILIS*

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(With 6 figures)

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INTRODUCTION

The dicynodont *Myosaurus gracilis* Haughton is known from several small skulls, some with associated postcranial remains, all from a single locality on the commonage of Harrismith, O.F.S., South Africa, where the remains of a *Lystrosaurus* zone (Basal Triassic) fauna occur in abundance. The genus is remarkable in that, until recently (Hotton 1974), it represented the only small-sized dicynodont form known to have survived the Permian-Triassic transition as recorded in the South African Beaufort succession. With an average skull length of 40 mm, *Myosaurus* is dwarfed by other South African Triassic dicynodont genera, such as its contemporary *Lystrosaurus* (typical skull length 100 mm) and the *Cynognathus* zone *Kannemeyeria* (typical skull length 400 mm).

In view of its almost isolated stratigraphic position, the cranial morphology and possible relationships of *Myosaurus* would appear to be matters of some interest, but after Haughton's (1917) description, no further preparation of the South African Museum type material was undertaken, with the result that, with the exception of the skull roof and occiput, the skull structure remains largely unknown. With the emphasis in dicynodont classification now increasingly involving areas other than the skull roof (Toerien 1953; Cluver 1970; Hotton & Cluver in press) it seemed that a detailed description of the material, including the palate, basicranium, braincase and lower jaw, would be necessary before the relationships of the genus could be adequately considered.

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In his original description, Haughton (1917) considered that *Myosaurus* was allied to *Emydops*, but differed in being free of molar or canine teeth; Van Hoepen (1934) came to a similar conclusion. Broom (1932) mentioned resemblances to *Cistecephalus*, from which, however, the genus differed in its small size and retention of the preparietal bone. The only other reference to the relationships of *Myosaurus* was made by Broom (1941) when describing *Myosauroides minnaari*, which he thought differed from *Myosaurus* mainly through its lack of a preparietal. *Myosauroides*, from the *Cistecephalus* zone, could, according to Broom, be placed '. . . somewhere between *Myosaurus* and *Cistecephalus*' (p. 210).

MATERIAL AND TECHNIQUES

In addition to the two co-type skulls (S.A.M. Nos 3526 and 3526a) in the South African Museum, five specimens were obtained on loan from the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; two of these latter specimens (B.P.I. Nos 2701b and 4269) have associated lower jaws. Disarticulated postcranial material is associated with the two type skulls, while B.P.I. No. 4269 has the articulated anterior third of the postcranial skeleton attached to the skull.

The bulk of the preparation was confined to the two type skulls, which are well preserved and virtually undistorted and which together complement each other to provide a complete picture of the skull morphology. These two specimens were completely cleared of matrix by means of automatic mallet and needle, and all areas, including the interior of the braincase, were made available for examination. Specimen 3526a had suffered a fracture across the back of the skull base during the original preparation, and it was thus also possible to clean out the inside of the left otic capsule. Preparation of the B.P.I. specimens was not carried to the same extent, and was mainly limited to exposure of the palate and, in two cases, the lower jaw.

Illustrations of the skull are orthoprojections; in the case of dorsal and ventral views the projections are on to a plane including the base of the foramen magnum and the ventral, inner surface of the nostril. The illustrations are mainly composite reconstructions of both co-type skulls, but, thanks to the almost total lack of distortion in the material, the reconstructions accurately represent the actual condition of the skulls.

In addition to these specimens of *Myosaurus*, the type (R.C. 54) of *Myosauroides minnaari* Broom was obtained on loan from the Rubidge Collection, and the palate and mandible prepared. A second, better preserved specimen of this species (A.M.N.H. 8209), loaned from the American Museum of Natural History, New York, yielded additional information after preparation. Several specimens of *Cistecephalus* in the collection of the South African Museum as well as the type and paratype (BMNH R4956, R4957) of *Emydops longus* in the British Museum (Natural History) London, were also used for comparison with both *Myosaurus* and *Myosauroides*.

CLASSIFICATION

For present purposes, the dicynodont classification of Haughton & Brink (1954), modified after Romer (1966) (see also Cluver 1974) can be most conveniently used to state the present systematic position of *Myosaurus gracilis*:

Class: Reptilia
Order: Therapsida
Suborder: Anomodontia (*sensu* Romer 1966)
Infraorder: Dicynodontia (*sensu* Romer 1966)
Family: Endothiodontidae (*sensu* Haughton & Brink 1954)
Subfamily: Pristerodontinae
Genus: *Myosaurus* Haughton

Diagnosis: Skull small, with relatively large orbits and weak snout. Intertemporal portion of skull roof wide. Postfrontals absent, pineal foramen relatively far back in skull roof. Squamosal flared sharply laterally above quadrate. Frontals and prefrontals make near-contact in midline ventrally to olfactory passage. Secondary palate long, no anterior palatal ridges. Palatine small, meeting premaxilla. Long vomerine septum dividing internal nares.

Myosaurus gracilis Haughton (1917)

Diagnosis: as for genus.

Co-types: Two skulls in nodule (S.A.M. Nos 3526 and 3526a) from Harrismith, O.F.S., South Africa.

Horizon/age: Lystrosaurus zone, Lower Triassic.

CRANIAL MORPHOLOGY OF *MYOSAURUS GRACILIS*

Skull roof

The nostrils are nearly terminal, and the anterior portion of the premaxilla, dividing the nostrils, is accordingly reduced to a delicate splint of bone, missing in most specimens. A short internasal process of the premaxilla extends back between the nasals, which may form slight bosses above and behind the nostrils. Behind the nostrils, and in front of the anterior border of the orbits, there is a slight narrowing or waisting of the snout, adding to the generally weak appearance of this anterior part of the skull. The septomaxilla is small, and confined to the interior of the nostril, where it forms part of the posterior wall. The maxilla rises fairly steeply behind the nostril, but is separated from the prefrontal by a narrow but persistent process of the lacrimal (Fig. 1B). The prefrontal is not strongly developed on the outer surface of the skull, and no boss is formed; the large orbit is thus almost circular in antero-lateral view.

The frontals (Fig. 1A) are important elements of the skull roof, meeting the nasals far forwards in an almost transverse suture, and extending back to a point level with the middle of the temporal fenestra. The pineal foramen lies
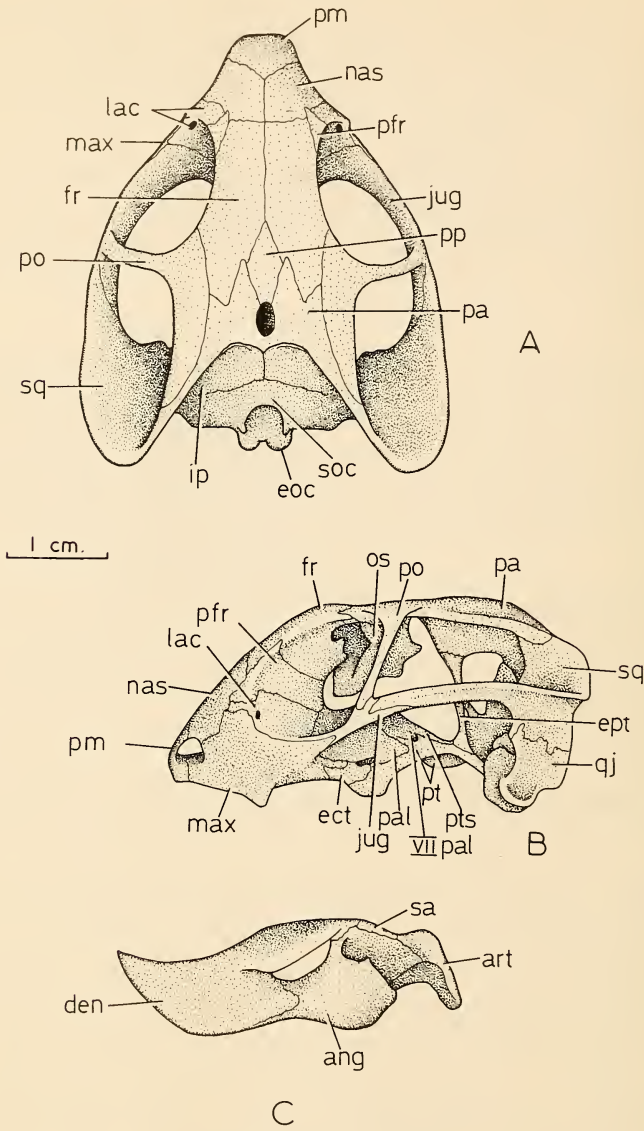
Fig. 1. *Myosaurus gracilis* × $\frac{3}{2}$. A–B. Skull in dorsal and lateral view respectively. C. Mandible in lateral view.

relatively far back in the skull, and there is a prominent, diamond-shaped preparietal.

Apart from the posterior portions of the frontals, the broad intertemporal region is composed of the parietals and postorbitals, a postfrontal being altogether absent (Fig. 1A). Each parietal is wide posteriorly, and bifurcates ante-
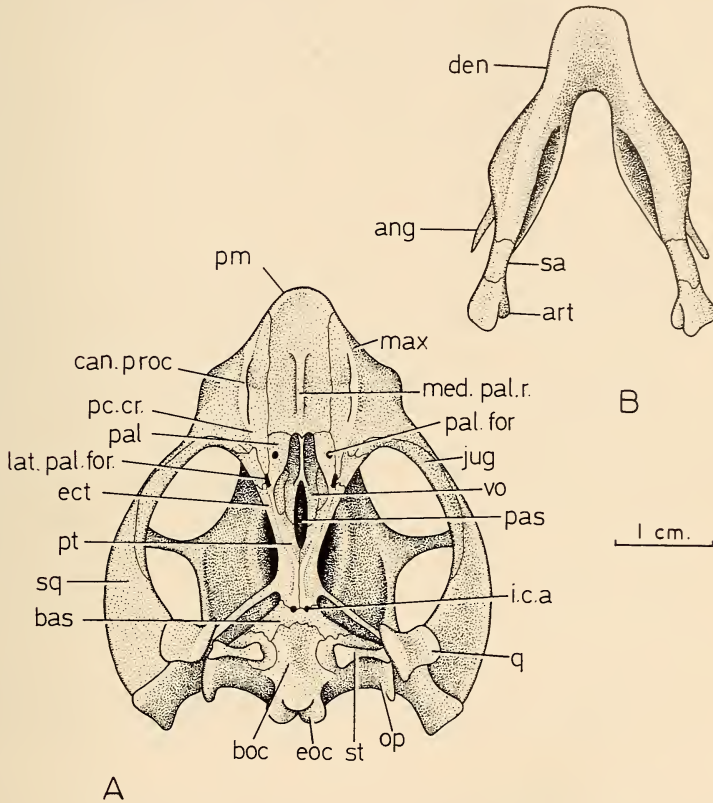

Fig. 2. *Myosaurus gracilis* × ³⁄₂. A. Skull in ventral view. B. Mandible in dorsal view.

riorly to surround the rear of the frontal of its side. Laterally it meets the post-orbital, which lies as a thin horizontal sheet over the upper part of the temporal opening. This part of the postorbital is essentially a lateral continuation of the parietal sheet, and therefore a bone of the dorsal skull roof. The lateral edge of the post-orbital is thickened and forms a stout dorsal border for the temporal fenestra.
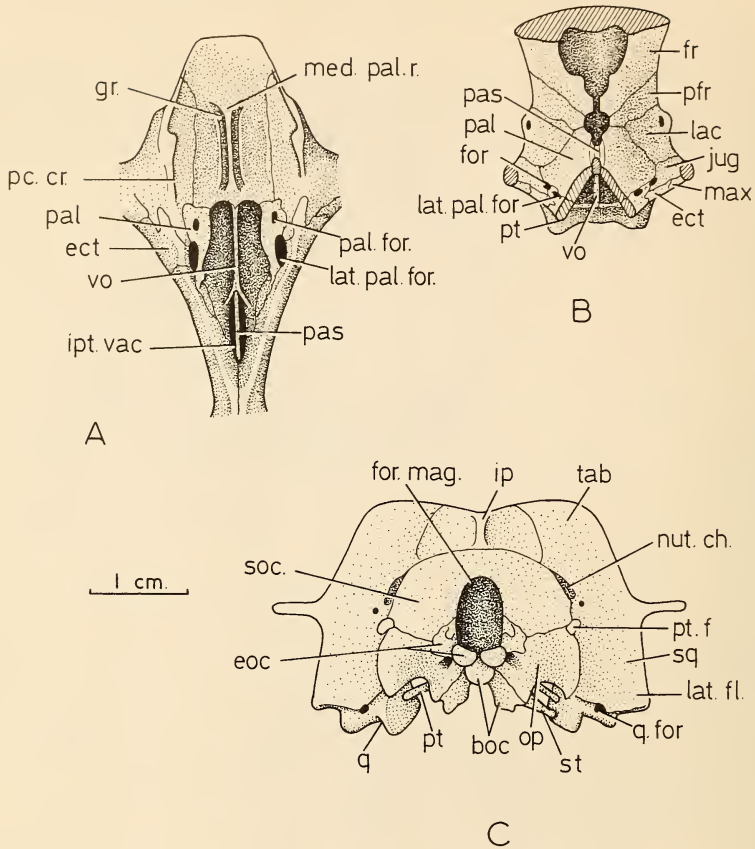
Fig. 3. *Myosaurus gracilis.* A. Palate in ventral view, × 2. B. Snout in posterior view, × $\frac{3}{2}$. C. Occiput, × $\frac{3}{2}$. Left stapes removed.

Occiput

The interparietal (Fig. 3C) lies wholly in the occiput, and does not overlap on to the skull roof, from which the occiput is clearly demarcated (Fig. 1A). A median crest divides the interparietal into two halves. Although not clear in all specimens, tabulars are present and lie as squarish plates on each side of the interparietal. The supraoccipital is clearly distinguishable from the surrounding dermal bones, and is on each side bounded by the crescent-shaped opening of a nutrient channel (Fig. 3C), similar to that found in *Lystrosaurus* (Cluver 1971). Each opening lies between the lateral edge of the supraoccipital and the medial edge of the squamosal and is closed off ventrally by a short inner lappet of the squamosal which makes a brief contact with the ventro-lateral corner of the supraoccipital. This process of the squamosal is pierced by a small foramen, which opens into the crescent-shaped space; directly below

lies the large posttemporal fenestra. It seems (Cox 1959; Cluver 1971) that all of these channels served for the forward drainage of blood from the neck musculature into the cranial cavity, prior to its discharge into the v. capitis lateralis and v. jugularis (see below).

The sutures between supraoccipital, exoccipital and opisthotic are clearly visible in occipital view. The exoccipital, carrying a process for articulation with the proatlas, is seen to have a limited lateral extent, so that the opisthotic meets the supraoccipital in a suture leading towards the posttemporal fenestra. The opisthotic is a stout bone, abutting against the squamosal laterally and notched for the passage of blood-vessels on the other three sides. Dorsally it closes off the posttemporal fenestra, through which passed the v. capitis dorsalis (Cox 1959); medially it forms the lateral wall of the jugular foramen and ventrally it is cut away for the course of the v. capitis lateralis.

The area of the braincase between the posttemporal fenestra and the jugular foramen is swollen, and stands out as a smooth bulge on the occiput. The exoccipitals meet in the midline ventrally, and form the posterior floor of the foramen magnum; the two exoccipital condyles overhang the basioccipital condyle to a quite considerable extent (Fig. 2A).

The squamosal forms the lateral border of the occipital plate in the usual way, but ventrolaterally it is drawn out as a prominent flange (Fig. 3C, lat. fl.) which extends out from directly above the quadrate. This is an unusual feature, not seen in other dicynodonts, and is most likely related to development of the lateral external jaw adductor muscle mass, for which the anterior face of this portion of the squamosal serves as an area of origin.

The quadrate (Figs 1B, 2A, 3C) is basically a vertical disc with a sharply offset lateral articular shelf, and the articular surfaces are at sharp angles to each other. The ventral, highly convex edge of the disc articulates with the medial articular process of the lower jaw, while the lateral, more gently convex lateral condyle meets the main articular surface of the articular bone. The two articular surfaces of the quadrate are separated by a sharply defined vertical step.

The quadratojugal is fused with the dorsal surface of the lateral quadrate condyle, and meets the squamosal dorsally in a highly interdigitating suture. A large quadrate foramen (Fig. 3C) lies between the quadratojugal and quadrate, and opens low down on the occiput between the rear of the lateral quadrate condyle and the ventral edge of the descending sheet of the squamosal.

The stapes (Fig. 2A) is a simple rod, inflated both proximally, to form a fairly distinct footplate, as well as distally, where it lies up against the inner side of the medial quadrate condyle.

Skull base and palate

In ventral view (Figs 2A, 3A), the skull displays several features of importance. The large fenestrae ovales are rimmed by the high, thin-walled basioccipital-basisphenoidal tubera. The porous nature of the bone surrounding each

Fig. 4. *Myosaurus gracilis*. Stereophotographs of: A. Braincase in ventral view (S.A.M. No. 3526). B. Interior of braincase showing left prootic and floccular fossa (S.A.M. No. 3256a). C. Palate (S.A.M. No. 3526a).

fenestra suggests the former presence of cartilage, in which the functional fenestra ovalis probably lay.

The pterygoids meet in the midline beneath the basisphenoid, anterior to the foramina for the internal carotid arteries, and a fairly strong median crest is formed. The slender quadrate ramus of each pterygoid extends back and laterally, terminating in a recess in the medial surface of the quadrate of its side (Fig. 3C). In front of their meeting in the midline, the pterygoids diverge laterally and form the outer borders of the long, vaulted choana. Anteriorly they meet the ectopterygoids and palatines of each side and terminate as fairly prominent, vertically expanded blades. Between each anterior pterygoid blade and the palatine is a sizeable, slit-like lateral palatal foramen; a freestanding ventral process of the palatine forms a part of the medial border of this foramen.

The palatal portion of the palatine is limited to a small, thin sheet, perforated by a large foramen (Figs 2A, 3A, pal. for.). This foramen, unusual in dicynodonts, opens into the interior of the choana above the horizontal portion of the palatine, where a second foramen between the palatine, jugal and ectopterygoid leads into the antero-ventral corner of the orbit in front of the upper opening of the lateral palatal foramen (Fig. 3B, for.). The palatal surface of the palatine is smooth, and its generally delicate construction, coupled with its apparent association with a blood-vessel or nerve, makes it doubtful whether it supported a layer of horn, as in other dicynodonts. The significance of this is more fully discussed below.

In the roof of the choanal vault the ventral edge of the parasphenoidal rostrum is visible in the long and narrow interpterygoidal vacuity. The vacuity is bounded anteriorly by the vomers, in normal dicynodont fashion; in front of this the two halves of the vomer are fused into a thin vertical septum which extends forwards to meet the premaxilla and divide the anterior part of the choana into two passages.

The premaxilla forms most of the secondary palate. It meets the palatine posteriorly and the maxilla is confined to an altogether lateral position. Anterior palatal ridges are lacking, but a median premaxillary ridge is a distinct feature. In section the ridge is T-shaped, with an inflated palatal portion supported by a thin vertical girder. On each side of the girder and parallel with it, the pre- maxilla is drawn out as a longitudinal crest, so that the median ridge is in effect flanked by a pair of partially enclosed channels (Fig. 3A, gr.). Anteriorly, where the median ridge merges with the general palatal surface, the grooves appear to diverge laterally without, apparently, penetrating the premaxilla, while posteriorly they lead towards an anterior notch in the choana, between premaxilla, palatine and vomer.

Similar premaxillary grooves have been described in other dicynodonts and it has been suggested (Cluver 1971) that they marked the passage of nutrient blood-vessels and/or nerves. On the other hand, the anterior choanal notch of dicynodonts, which the grooves approach in *Myosaurus*, has been indicated as the most likely point of emergence of the duct of Jacobson's organ (Cluver 1971),

and the condition in *Myosaurus* could perhaps be interpreted as indication of a doubling back, in an anterior direction, of the duct to an opening in the primitive forward position. Equally possible, however, is an association between the premaxillary grooves and the palatine foramina, and with the lack of conclusive evidence the question must remain unresolved.

The palate is bounded laterally and anteriorly by a modest rim, which is drawn down to a small but clear maxillary caniniform process. The medial surface of this rim has a shallow depression in front of the caniniform process, but this is not the deeply incised palatal notch of '*Dicynodon*' *testudirostris* (Cluver 1970; Hotton & Cluver in press), nor is any caniniform flange present. Between the rear of the caniniform process and the expanded pterygoidal sheet on the choanal border, the palatal rim is at first a fairly sharp postcaniniform crest, and then becomes a low and smoothly rounded ridge, formed by the maxilla and the small, tightly interdigitated ectopterygoid. As with the palatine, the palatal surface and rim is nearly devoid of nutritive foramina and channels, and the pitting and rugoseness of other dicynodont palates is absent.

Braincase, basicranial axis and orbit

The otic capsule is the most prominent part of the preserved bony braincase. The opisthotic and exoccipital portion is inflated posteriorly above the jugular foramen, as stated above, while in front the prootic is laterally displaced to accommodate what appears to have been a relatively large brain. That the structures of the brain were closely apposed to the walls of the braincase is further suggested by the presence of a very deep floccular (sub-arcuate) fossa in the rear of the prootic (Fig. 4B). This fossa is remarkable in that it communicates, by means of a fairly large opening, with the vestibule of the inner ear (see below). On its anterior, outer face the prootic is deeply incised between the posttemporal fenestra and the posterodorsal corner of the braincase, and below its meeting with the parietal the prootic is cut away to form a very distinct notch leading into the interior of the braincase. A very clearly demarcated channel for the v. capitis dorsalis (Cox 1959; Cluver 1971) is thus formed. As the posttemporal fenestra opens more or less directly into the ventral part of this passage, and as the prootic shows no comparable groove below the fenestra, it appears that most of the blood from the occiput passed into the v. cephalica posterior within the braincase (Dendy 1909; Swain 1968); a limited portion only would probably have flowed down through a sinus below the posttemporal fenestra to meet the v. capitis lateralis.

Within the braincase, the pair of posterior cephalic veins would have been joined by the small occipital veins passing forwards between the supraoccipital and interparietal (see above) before descending to issue from the skull as the jugular veins. There is a deep hollow in the inner surface of the parietal in the postero-dorsal corner of the braincase above the foramen magnum, and it seems likely that in life this was filled by a dorsal cartilaginous extension of the supraoccipital, similar to that of *Lystrosaurus* (Cluver 1971); the pair of occipital veins would probably have entered the cranial cavity at this level.

Several inner ear structures can be made out. The fenestra ovalis is relatively very large (Fig. 4A), but was probably furnished with a cartilaginous rim during life. From the fenestra ovalis a short, wide chamber leads to the vestibule. This chamber, which may be called the perilymphatic chamber, is medially expanded below the vestibule of the inner ear, and is unlike the simple auditory tube of other dicynodonts, which links the fenestra ovalis with the deep structures of the inner ear. It appears that in *Myosaurus* a fairly large footplate, perhaps partly cartilaginous, was associated with a considerably expanded perilymphatic sac or cistern. Inside the braincase the internal auditory meatus is confluent with the inner opening of the jugular canal, so that at this point the otic capsule is separated from the skull base by a wide space, leading to the jugular canal behind, the fenestra ovalis ventrally and the vestibule and succulocochlear recess medially. A relatively large recess, which housed the ampullae of the horizontal and anterior vertical semicircular canals, is visible, and it appears that the utriculus lay in a dorsal cavity fairly clearly demarcated from the wider saccular space below.

The floccular fossa opens into the utricular cavity, as stated above. This appears to be a unique condition. Olson (1944) states that the anterior vertical semicircular canal was in many cases confluent with the floccular fossa in his sectioned dicynodonts, but in *Myosaurus* this is not the case, and the canal in question arises far forwards of the inner opening of the fossa. It seems very unlikely that a direct communication between the interior of the otic capsule and the cranial cavity ever existed, and capsule and fossa were almost certainly membraneously separated during life.

Close in front of the internal auditory meatus lies a foramen, in the position of the internal opening of the VIIth (facial) nerve (Olson 1944; Cluver 1971). A short and narrow canal leads into the foramen from the anterior, saccular part of the vestibule, below the anterior ampullary recess, so that there appears to be a connection between the otic capsule and the facial canal. Comparison with a *Lystrosaurus* braincase (S.A.M. No. 11180; see also Cluver 1971) shows that in this genus a deep and narrow cleft leads from below the front of the anterior ampullary recess to the region of the facial nerve foramen, while what appears to be a similar cleft can be seen in some of Olson's (1944) sectioned dicynodonts. Closure and canalization of such a cleft up to the level of the facial foramen would lead to a condition similar to that seen in *Myosaurus*, but the function of the cleft or canal remains obscure. While in a form such as *Lystrosaurus* the cleft could have supported a portion of the perilymphatic duct system, in *Myosaurus* the canal apparently enclosed a nerve, blood-vessel or duct, which then, presumably, either emerged into the anterior part of the braincase alongside the root of the facial nerve, or passed down the facial foramen to leave the braincase with the cranial nerve. Serial grinding of a *Myosaurus* braincase would seem to offer the only means of resolving the question.

No fenestra rotunda appears to have been present, and the perilymphatic duct probably terminated in the jugular foramen, as suggested by Olson (1944).

The floor of the braincase, formed by the basioccipital and basisphenoid, is smooth and flat, and a dorsum sellae is altogether absent. The paired internal carotid arteries enter the interior of the skull through a wide common opening, which probably housed a ventral part of the hypophysis as well. A true fossa hypophyseos is absent. Alongside this opening the ossified bases of the pilae antoticae of the prootics extend up as a pair of relatively long and stout pillars, inclined slightly forwards. Immediately lateral to each pillar lies the slender epipterygoid, rising from its footplate to meet a broad, descending flange of the parietal. This sheet of the parietal, together with the epipterygoid and ossified pila antotica, forms an incomplete sidewall to the brain cavity at the hypophysis-pineal organ level.

Immediately in front of the inner opening of the internal carotid artery lies a low bony septum, identified as a separate presphenoid element by Cluver (1971) but regarded as an anterior basisphenoidal extension by some authors (Broom 1926; Cox 1959). In *Myosaurus* the presphenoid (Figs 1B, 3B) is clasped by the trough-like cultriform process of the parasphenoid and, as shown in *Lystrosaurus* (Cluver 1971), was probably connected to a more extensive cartilaginous interorbital septum at its abrupt anterior truncation. Laterally and ventrally the parasphenoid is firmly held by the pterygoids up to the latter's meeting with the palatines. At this point a slit-like foramen is formed on each side between the pterygoid and the side of the parasphenoid-presphenoid septum (Fig. 1B, VII pal.), and presumably served for the exit of the ramus palatinus of the VIIth (facial) nerve.

Anterodorsally the neurocranium is represented by the ossified orbito-sphenoid-mesethmoid complex (Fig. 1B, os). This complex is best seen in S.A.M. No. 3526a, where it has been displaced into a position suitable for detailed preparation. The orbitosphenoid is a wide trough, with a ventral notch posteriorly for the exit of the pair of optic nerves, and bears a prominent ventral keel which is deepest anteriorly. This part of the complex, lying up against the ventral surface of the frontals, presumably housed part of the olfactory lobes. The mesethmoid, a short but deep septum clearly distinguishable from the orbito-sphenoid, divides the pair of olfactory channels as they pass forwards into the snout.

Only a short space separates the mesethmoid from the anterior, inner wall of the orbit. *Myosaurus* is unusual among dicynodonts in that the frontal, prefrontal and lacrimal, which normally surround a wide, anterior orbitonasal opening leading into the snout, have undergone an extensive medial develop-ment, the frontals in fact almost meeting in the midline below the olfactory opening (Fig. 3B). The interior of the snout is thus, with the exception of the olfactory opening, almost completely closed from the orbit; a small, almost circular space between the prefrontals probably represents an orbitonasal opening reduced from the usual dicynodont condition (see e.g. *Lystrosaurus*, Cluver 1971). Ventrally the palatines meet the prefrontals near the midline, thereby excluding the lacrimal from the border of the orbitonasal opening.

Below and behind the orbitonasal opening the palatines lie closely apposed to the parasphenoidal rostrum, so that the midline region is completely floored by bone.

Lower jaw

The symphyseal region, usually powerfully developed in dicynodonts, is relatively weak in *Myosaurus* (Figs 1C, 2B). There are no dentary tables and the very slightly concave dorsal dentary surface is scooped out in front to form a deep cleft behind the anterior shovel-shaped tip. This anterior edge is not well preserved in any specimen, but indications are that it was at least fairly sharp. The weak development of the dentaries is reflected in the considerable exposure of the splenials in anterior view.

A fairly prominent lateral dentary shelf is formed in front of and above the mandibular fenestra, while the rear half of the dentary's dorsal surface, behind the slightly grooved anterior portion, is narrow and smoothly rounded. The anterior surface of the dentary, below the shovel edge, is heavily pitted by nutritive foramina, and indications are that a horny sheath covered this front part of the lower jaw. No such pitting can be detected on the dorsal edges of the dentary, where clear evidence of a horn covering is usually found in dicynodonts.

The jaw is deepest in the angular region, even when the extensive reflected lamina of the angular is not taken into consideration. In the rear of the jaw the articular is seen to be drawn down ventrally into a long and powerful retro-articular process, but little else, especially of the inner surfaces, can be made out.

JAW FUNCTION IN *MYOSAURUS*

The jaw musculature of dicynodonts has been reconstructed by Crompton & Hotton (1967). From subsequent comparisons (Cluver 1970, 1971) it appears that the area of greatest variation in this system lies in the nature of the insertion of the external adductor muscles on the lower jaw. Two divisions of the external adductor musculature were present in dicynodonts, these being a medial external adductor arising from the bones surrounding the temporal fenestra, and a lateral external adductor arising from the anterior surface of the descending squamosal sheet and the ventral surface of the squamosal's zygomatic bar. Crompton & Hotton (1967) suggest that in dicynodonts such as *Lystrosaurus* and *Emydops* the medial mass inserted into a groove in the dorsal surface of the dentary behind the dentary tables, while the lateral mass was attached to a lateral dentary shelf lying above and partly in front of the mandibular fenestra. However, it appears that in certain genera (Cluver 1970, 1971) the groove and shelf are absent or present only in modified form, and it has been suggested (Cluver 1974) that an additional slip of the external adductor muscle inserted around the dorso-lateral margin of the adductor fossa, on the inner side of the jaw ramus.

In *Myosaurus* no dorsal dentary groove is found, but a prominent lateral dentary shelf is present, and the dentary is powerfully buttressed over the

mandibular fenestra. The lateral external adductor muscle was therefore pro-
vided with a well-defined area of attachment, but the limits of the insertion
area of the medial group are less clear; this muscle probably attached on the
inner surface and the rounded dorsal edge of the dentary, behind its horn-
covered anterior portion.

The possible range of jaw movements in small edentulous dicynodonts
such as *Cistecephalus* have been recently discussed (Cluver 1974) and it has
been shown that the typically wide cistecephalid palate, narrow symphyseal
region and relatively flat quadrate and articular articulation surfaces could
indicate lateral movement across the palate during the anteroposterior cycle
of jaw movements as described in dicynodonts by Crompton & Hotton (1967).
In this respect, however, *Myosaurus* appears to have retained the primitive
range of movements: the articular surfaces of the quadrate are at sharp angles
to each other and quadrate-articular rotation appears to have been highly
unlikely. In addition, the long and narrow secondary palate, with rim and canini-
form processes hardly wider than the symphyseal area of the lower jaw, suggests
that upper and lower apposing surfaces would have met during strictly antero-
posterior sliding movements.

The nature of these occluding surfaces, however, is unusual. As shown
above, the dentaries are weakly developed anteriorly, and there are no dentary
tables such as appose the palatine and maxilla in *Lystrosaurus* and *Dicynodon*
(Cluver 1970, 1971). At the same time, a battery of mandibular teeth, which
bite against the palatine in forms such as *Emydops*, is absent, and the apparent
lack of a horn covering in the palatine region, as well as the delicate structure
of that bone, appears to be a consequence of this.

The only clear evidence of horn is found on the anterior surface of the
fused dentaries, and points to the presence of a horny sheath over the sharp-
edged, square tip of the symphysis. Behind this the lateral edge of the dentary,
bordering the slightly concave dorsal surface, is fairly sharp and may have
carried a posterior extension of the beak. While the shovel-like tip would have
acted against the anterior premaxillary surface, as suggested by the absence of
anterior palatal ridges, the more lateral parts of the lower beak would have
had some slicing effect against the palatal rim, which, in turn, was probably
furnished with a corresponding horny layer. It seems unlikely, in view of the
smooth bone surfaces involved, that either of these lateral horn coverings were
substantial or extended as far medially as the median palatal ridge with its pair
of flanking channels.

The dietary preferences of an animal such as *Myosaurus* can only be
speculated upon. Certainly, the lack of well-developed shearing and crushing
areas in the mouth suggests a food source very different to the presumably
fairly coarse vegetation for which the contemporary *Lystrosaurus* was equipped.
Cox (1972) has recently suggested that the small cistecephalid *Kawingasaurus*
fed upon soft-bodied, and presumably slow-moving, invertebrates, and a
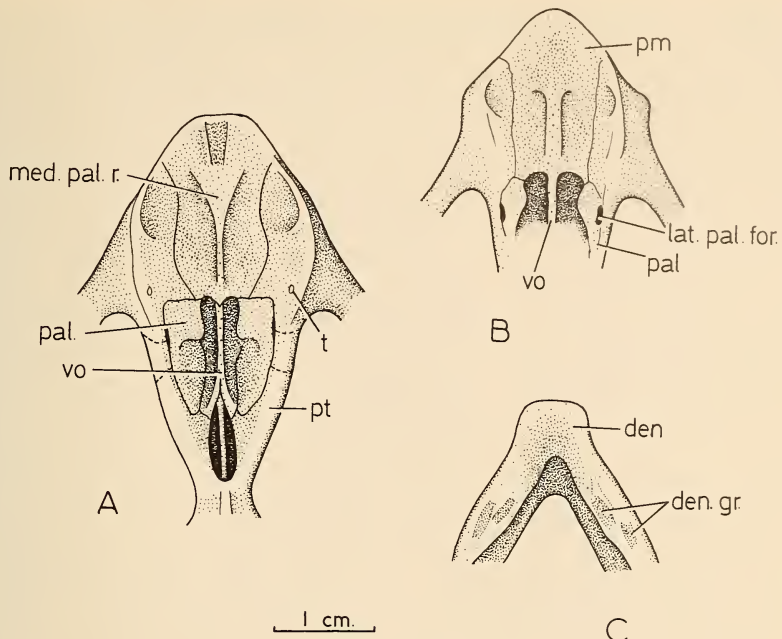roughly similar diet in the case of *Myosaurus* cannot be ruled out.

Fig. 5. A. *Emydops longus* paratype B.M.(N.H.) R4957. Palate, $\times$ $\frac{3}{2}$. B–C. *Myosauroides minnaari* type R.C.54, $\times$ $\frac{3}{2}$. Anterior palate and dorsal view of mandible respectively.

COMPARISON WITH OTHER DICYNODONTS

At present, three genera especially appear to have significant resemblances, and possible affinities, with *Myosaurus*. These are *Emydops*, *Cistecephalus* and *Myosauroides*.

The Upper Permian *Emydops* (Fig. 5A) has been mentioned as a possible *Myosaurus* ancestor by Haughton (1917) and, although the genus has many clearly primitive characters, it does include features which deserve consideration. These are a definite palatine-premaxilla contact, a long narrow interpterygoidal vacuity, and a thin, steep vomerine septum dividing the internal nares. The palatine, in contrast to *Myosaurus*, is still well developed and received the bite of the lower jaw teeth during mastication, but in the upper jaw teeth are vestigial and apparently of no great functional significance. In the skull roof the proportions of intertemporal to interorbital width are close to those of *Myosaurus*, but the postorbital is not flared laterally above the temporal fenestra and instead forms the vertical border of the intertemporal bar. A large postfrontal, lost in the more progressive smaller genera, is still present, as is the preparietal. The lower jaw has a row of functional teeth on the medial edge of the dentary, but anteriorly no dentary table is formed and a shovel-like tip, basically similar to that of *Myosaurus*, is formed.

Clearly, *Emydops* itself should not be designated a direct ancestor of *Myosaurus*, but it does none the less possess several characters expected in such an ancestor, and it seems very likely that a more detailed knowledge of *Emydops* and allied forms would reveal a more definite picture of the origins of later groups such as *Myosaurus*.
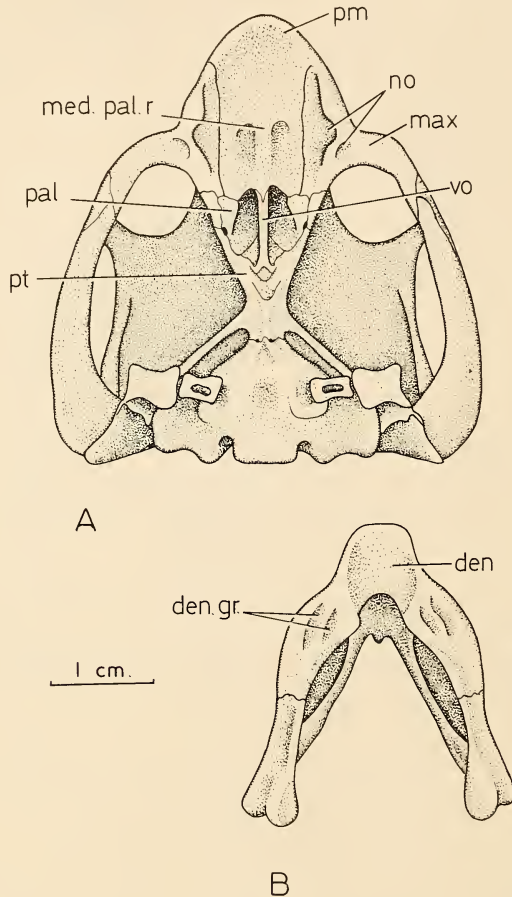

Fig. 6. *Cistecephalus* sp. S.A.M. No. 10665 × $\frac{3}{2}$. A. Ventral view of skull. B. Dorsal view of mandible.

The genus *Cistecephalus* has recently been reviewed by Keyser (1973) and discussed by Cluver (1974), and the skull morphology is now well known (Fig. 6). While there are obvious adaptations to a specialized way of life, several resemblances to *Myosaurus* exist. A postfrontal is absent, as in *Myosaurus*, but the exceptionally wide intertemporal sheet lacks a preparietal. Ventrally

the secondary palate has very much the same organization as *Myosaurus*, and anterior palatal ridges are absent and the maxilla is confined to a lateral position. The palatines are small and, as in *Myosaurus*, each is pierced by a foramen. In the lower jaw the dentaries are drawn up anteriorly to a transverse blade, fairly sharp, while laterally a prominent dentary shelf is formed.

Here, however, the similarities cease. In *Cistecephalus* the interpterygoidal vacuity has been obliterated by reinforcement of the basicranial girder, and the vomer is a deep and wide plate with its ventral edge level with the ventral borders of the pterygoids. Anteriorly, two pairs of pockets, one lateral and one medial to the palatal rim, lie at the level of the weak caniniform process; these pit-like depressions seem to be unique to *Cistecephalus*. A wide orbitonasal opening leads into the interior of the snout, while the lacrimal foramen (if present) is unusually placed near the border of this opening. The lower jaw, again, is more powerfully developed in *Cistecephalus* than in *Myosaurus*, and the deep symphyseal region is characteristically scooped out behind the square, shovel-like tip; the dorsal surface of each dentary is widely expanded behind this, and very different to the narrow, weakly developed dentary ramus of *Myosaurus*. When, in addition to these factors, the perforated stapes and secondary widening of the skull roof are taken into consideration, it becomes clear that descent of a form such as *Myosaurus* from this genus is highly improbable, even although certain apparently significant resemblances between the two genera exist.

Myosauroides, the third genus which can be conveniently compared with *Myosaurus*, shows resemblances to both that genus and *Cistecephalus* (Fig. 5B, C). The intertemporal region is of the same width as in *Myosaurus* and also lacks a postfrontal, while a ventral flange of the frontal extends medially in a manner reminiscent of *Myosaurus*. Anterior palatal ridges are lacking, the palatine is weak, and the interpterygoidal vacuity and delicate vomerine septum are almost identical to the *Myosaurus* condition. The jaw symphysis has the same sharply squared-off tip, and the stapes is the usual thin, unperforated rod. *Myosauroides* has a fairly prominent caniniform process and a higher palatal rim than *Myosaurus*, but this rim is continued posteriorly from the caniniform process for a short way as a postcaniniform crest, similar to that of *Myosaurus*. Differences from *Myosaurus*, which are at the same time resemblances to *Cistecephalus*, are the broad, grooved dorsal dentary surfaces, the lack of a preparietal, and the generally still wide orbitonasal passage.

Of the three genera, *Myosauroides* appears to be the closest to *Myosaurus*, and it is quite conceivable that, with the exception of the preparietal, characteristics of *Myosaurus* such as the highly reduced orbitonasal passage and the weak dentary ramus could have been derived from the *Myosauroides* condition. In terms of jaw function, too, *Myosaurus* and *Myosauroides* appear to be broadly similarly adapted, and there is no evidence in *Myosauroides* of lateral jaw displacement during mastication such as is found in *Cistecephalus* (see above). The quadrate-articular surfaces are tightly interlocked and the secondary

palate is not significantly wider than the symphyseal region of the lower jaw. However, the lack of a preparietal precludes *Myosauroides minnaari* itself from direct ancestry of *Myosaurus*.

Viewed generally, the three genera *Myosaurus*, *Myosauroides* and *Cistecephalus* appear to be united by fairly clear common characteristics, with *Myosaurus* and *Myosauroides* more closely related to each other than either is to the strongly divergent *Cistecephalus*. If these genera are indeed part of a natural group, this is not reflected in any present classification, where *Cistecephalus* and *Myosaurus*, for instance, are usually placed in separate families (Haughton & Brink 1954; Boonstra 1972; Cluver 1974). In view of the fact, however, that a common origin of the group cannot as yet be convincingly established, and as our knowledge of the many Permian pristerodontinid genera is still very incomplete, it seems unwise to attempt any large-scale classificatory reorganization of the endothiodontids at present.

SUMMARY

The skull of *Myosaurus gracilis* shows several departures from the usual dicynodont condition, especially in the otic capsule, snout, secondary palate and mandible. Perhaps in keeping with its lone survival into the early Triassic, most of these modifications are connected with mastication, and seem to reflect a dietary change. *Myosaurus* shares such features as a broad inter-temporal region, lack of a postfrontal, the small palatine and laterally confined maxilla, as well as the absence of anterior palatal ridges and the presence of a square-tipped, shovel-shaped jaw symphysis, with Upper Permian genera such as *Myosauroides* and *Cistecephalus*. While there is a possibility of these three genera belonging to a single natural group, their relationships with the numerous and generally poorly-known Permian endothiodontids remain obscure, and a reorganization of the classification of the Endothiodontidae has not been attempted. Among themselves, *Myosaurus* and *Myosauroides* show the closest relationship, while the more aberrant *Cistecephalus* is strongly specialized in respect of, especially, the skull roof, basicranial axis and palate-mandible relationships.

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ABBREVIATIONS

ang.	angular	pal. for.	palatine foramen
art.	articular	pas.	parasphenoid
bas.	basisphenoid	pc. cr.	postcaniniform crest
boc.	basioccipital	pfr.	prefrontal
can. proc.	caniniform process	pm.	premaxilla
den.	dentary	po.	postorbital
den. gr.	dentary gr.	pp.	preparietal
ect.	ectopterygoid	prs.	presphenoid
eoc.	exoccipital	pt.	pterygoid
ept.	epipterygoid	pt. f.	posttemporal fenestra
for.	foramen	q.	quadrate
for. mag.	foramen magnum	q. for.	quadrate foramen
fr.	frontal	q.j.	quadratojugal
gr.	groove	sa.	surangular
i.c.a.	internal carotid artery opening	soc.	supraoccipital
ip.	interparietal	sq.	squamosal
ipt. vac.	interpterygoidal vacuity	st.	stapes
jug.	jugular	t.	tooth
lac.	lacrimal	tab.	tabular
lat. fl.	lateral flange of squamosal	A.M.N.H.	American Museum of Natural History, New York
lat. pal. for.	lateral palatal foramen	B.M.(N.H.)	British Museum (Natural History), London
max.	maxilla		
med. pal. r.	medial palatal ridge on premaxilla	B.P.I.	Bernard Price Institute for Palaeontological Research, Johannesburg
nas.	nasal		
no.	notch		
nut. ch.	nutrient channel	R.C.	Rubidge Collection, Graaff-Reinet
op.	opisthotic		
os.	orbitosphenoid	S.A.M.	South African Museum, Cape Town
pa.	parietal		
pal.	palatine		